Do Gulf of Alaska fish and crustacean populations show synchronous non-stationary responses to climate?

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A B S T R A C T

Changes in the abundance and productivity of biological populations in the North Pacific have often been associated with large-scale modes of climate variability. The Pacific Decadal Oscillation (PDO), which describes spatio-temporal variability in North Pacific sea surface temperature (SST), correlates with much of this variability. However, since the late 1980s, the North Pacific Gyre Oscillation (NPGO) has explained an increasing proportion of variance in North Pacific climate properties. Ecological responses to this change in the proportion of variance ascribed to the two climate patterns remain poorly understood. Here, we test the hypothesis that relationships between biological time series and climate covariates (SST and the PDO) differ for nine Gulf of Alaska fish and crustacean populations before and after the late 1980s. Additionally, we evaluate whether non-stationary climate-biology relationships arose synchronously across populations as a community response. We used different formulations of Generalized Additive Models in a population and community context and compared results to the classical approach of aggregated population responses based on Principal Component Analysis (PCA). The results showed that climate-biology relationships weakened or reversed for most populations in the late 1980s, coinciding with the increase in variance of the NPGO. However, these non-stationary responses were highly species-specific and did not arise synchronously as a community response. We show that PCA does not represent community dynamics properly when only few species covary in time and exhibit long-term trends. Therefore, this approach might not be always useful to detect synchronous changes among biological time series as a community response. Novel associations among climate variables and novel climate-biology relationships are expected to become increasingly evident with future climate change, and the recognition of switches between different explanatory variable-response relationships may be critical for successful management of marine resources during transitions to these novel climate states.

1. Introduction

Low-frequency shifts in North Pacific climate have significant impacts on marine ecosystems (Di Lorenzo et al., 2008; Hare and Mantua, 2000; Yeh et al., 2011). Community variability aggregated across multiple populations of salmon, groundfish, crustaceous zooplankton, gelatinous zooplankton and decapod crustaceans has often been correlated with variability in the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (Hare and Mantua, 2000; Litzow, 2006; Litzow et al., 2014; McFarlane et al., 2000; Overland et al., 2008). The PDO represents the dominant mode of variability in

detrended North Pacific sea surface temperature (SST), which is primarily forced by the Aleutian Low pressure system (Newman et al., 2016). Biological productivity and SST variability captured by the PDO have often covaried over time, resulting in time series of biological productivity with a changing mean values associated with abrupt changes between persistent PDO regimes (Hare and Mantua, 2000; Litzow et al., 2014). For instance, Pacific salmon (*Oncorhynchus* spp) catches in the Gulf of Alaska (GoA) increased after the 1977 climate shift when the PDO state changed from a cold to a warm regime in the northeast Pacific (Hare and Mantua, 2000; Litzow et al., 2014).

Particularly notable shifts in North Pacific climate and biology time

series occurred in 1976/77 and 1988/89 (Hare and Mantua, 2000). Several studies (Di Lorenzo et al., 2008; Hare and Mantua, 2000; Yeh et al., 2011) have pointed out that the 1989 shift was not a reversal of the PDO state, and the North Pacific did not return to the physical and biological conditions that existed prior to 1977 (Di Lorenzo et al., 2008; Hare and Mantua, 2000; Yeh et al., 2011). The 1988/89 climate shift has mostly been defined as a shift in the second axis of North Pacific climate variability, which is now most commonly defined with the NPGO (Bond et al., 2003, Di Lorenzo et al., 2008). Several other studies have shown that the late 1980s began a period of increasing variance in the NPGO and/or an increasing association between the NPGO and the first axis of North Pacific climate variability (Di Lorenzo et al., 2010, Litzow et al., 2018; Yeh et al., 2011, Sydeman et al., 2013). However, the ecological implications of these changes in NPGO variability have received relatively little attention. One important feature of this change appears to have been a decline in the temporal variability in sea level pressure (SLP) anomalies associated with the Aleutian Low after the late 1980s (Litzow et al., 2018). This decline in Aleutian Low variability apparently had important implications for the strength of collinear relationships among individual environmental variables in the Gulf of Alaska (GoA). Prior to the late 1980s, under high Aleutian Low variance, SST anomalies associated with the PDO showed strong covariance with a range of other GoA variables related to the strength of cyclonic circulation associated with the Aleutian Low, including a SLP gradient associated with southwesterly (onshore) winds, orographic precipitation, coastal freshwater discharge and coastal salinity, coastal downwelling, wind stress patterns, and gyre-scale advection (Stabeno et al., 2004, Weingartner et al., 2005). When Aleutian Low variance declined after the late 1980s, collinearity among these environmental variables also declined (Litzow et al., 2018). At the same time, previously strong covariance between climate (SST and the PDO) and productivity in GoA salmon (*Onchorynchus* spp) declined to zero (Litzow et al., 2018). The degree to which climate-biology relationships changed for other GoA taxa at this time is unknown. Changes to the climate-biology relationships that characterized the GoA system for most of the 20th century would have important implications for our ability to predict ecological responses to climate change in that system (Schmidt et al., 2014; Wolkovich et al., 2014).

Here, we hypothesize that fish and crustacean populations in the GoA exhibit non-stationary relationships with North Pacific climate variability as demonstrated by a shift in the explanatory variable-response relationship, which is associated with the change in the relative importance of PDO and NPGO patterns. A key and novel characteristic of our analyses is that of considering changes in covariance between explanatory and response variables as opposed to only changes in the mean or variance of the response variables. To address our hypotheses, we develop a new approach to analyze species responses to climate variability in a community context, which may be broadly applicable to other systems. Our approach consists of (1) comparisons of stationary models (in which climate-biology relationships are assumed to be constant across the time period considered, 1960s – 2010s) with non-stationary models in which the climate-biology relationship is allowed to vary across an objectively selected threshold year. Then, (2) we assess whether non-stationary relationships across populations might arise synchronously, and therefore result in a community response. Finally, (3) we compare our results with those obtained from the classical approach of aggregated species responses based on PCA.

2. Methods

2.1. Biological data

We analyzed nine biomass or recruitment time series from the Gulf of Alaska (Table 1). The time series include: crustaceans (2), forage fish (2) and groundfish (5) species. Recruitment time series (in number of individuals) were obtained from the GoA stock assessment reports of

Table 1

Summary of the time series for the fish and crustacean populations in the Gulf of Alaska. Years for biomass indices correspond with survey data and those for recruitment with assessment data lagged to age zero.

Common name	Scientific name	Index	Years
Shrimps	Pandalidae	Biomass	1972–2015
Tanner crab	*Chionocetes bairdi*	Biomass	1972–2015
Capelin	*Mallotus villosus*	Biomass	1972–2015
Herring	*Clupea pallasii*	Biomass	1968–2011
Pacific cod	*Gadus macrocephalus*	Biomass	1972–2015
Sablefish	*Anoplopoma fimbria*	Recruitment	1969–2011
Walleye pollock	*Gadus chalcogrammus*	Recruitment	1969–2012
Pacific ocean perch	*Sebastes alutus*	Recruitment	1975–2010
Arrowtooth flounder	*Atheresthes stomias*	Recruitment	1969–2011

the Alaska Fisheries Science Center (AFSC; www.afsc.noaa.gov/refm/stocks/assessments.htm). The rest of the population time series were obtained from the small mesh bottom trawl surveys conducted annually by the U.S. National Marine Fisheries Service and the Alaska Department of Fish & Game in the entire western GoA (see details in Anderson & Piatt 1999). Catch per unit effort (CPUE) data used from the small mesh survey were log-transformed biomass (kg·km^{-1} towed) for fish and shrimp and log-transformed counts (individuals·km^{-1}) for Tanner crabs. Biomass is considered a reasonable proxy for biological productivity in short-lived species such as shrimps and forage fish. However, we used counts in the Tanner crab analysis since this metric better represents the abundance of young age classes and thus is a better proxy for biological productivity in this longer-lived species. Recruitment data of Pacific cod from the assessment reports were too short for the purpose of this study. Therefore, we used biomass data from the small mesh survey since total CPUE is sensitive to annual-scale climate variability in this species (Anderson and Piatt, 1999; Litzow and Ciannelli, 2007), presumably because of inshore distribution changes that are responsive to temperature. The ensemble of the fish and crustacean population time series that we included in this study is likely to capture short-term population responses to climate variability (Anderson and Piatt, 1999; Litzow and Ciannelli, 2007; Zheng and Kruse, 2000). All the recruitment time series were log transformed and lagged to the cohort year (i.e. age 0), and all time series were normalized (i.e., subtracted the mean and divided by the standard deviation) prior the analyses to make magnitudes comparable.

2.2. Environmental data

Sea surface temperature and climatic indices such as indices for regional SST, the PDO, the Aleutian Low, or NPGO, have been traditionally used as explanatory variables of the population and community variability in the Northeast Pacific (Anderson & Piatt, 1999; Hare and Mantua, 2000; Litzow, 2006; McFarlane et al., 2000), due to their availability and association (understood as potential proxies) with other processes (e.g. upwelling, advection) that influence biological communities (Litzow et al., 2018). For similar reasons and in order to compare our results with previous studies, we used PDO and Gulf of Alaska SST as explanatory variables in the analyses.

The PDO Index is defined as the leading principal component of North Pacific monthly SST anomalies, poleward of 20 N, after the global mean SST anomaly is removed from each North Pacific grid cell, for the fixed reference period of 1900–1993 (http://research.jisao.washington.edu/pdo/PDO.latest). Since we hypothesized that non-stationary relationships might arise from a change in the climate state of the North Pacific (PDO-type to NPGO-type), we also analyzed shifts of fish and crustacean populations and community responses directly to SST. Monthly data of GoA SST (available from NOAA extended reconstructed SST at www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v4.html) were transformed to anomaly values of the area included between 54

and 62° N and 134-160° W. PDO index and GoA SST values were averaged over the winter months (NDJFM) and smoothed with a 3-yr running mean (Supp.1) to capture variability at a biologically effective time scale (Di Lorenzo and Ohman, 2013).

Additionally, we evaluated changes in the importance of the PDO and NPGO patterns in North Pacific climate by calculating EOF1 of North Pacific SST anomalies (20–66 N, 132E – 130 W, seasonal signal removed and anomalies detrended, cells weighted by area) for the periods 1950–1988 and 1989–2012. We then correlated this era-specific leading axis of variability with downloaded values of PDO and NPGO indices, using the Modified Chelton method to account for temporal autocorrelation in the data (Pyper and Peterman, 1998).

2.3. Detecting non-stationary relationships

We contrasted two different Generalized Additive Models (GAM) formulations to identify the type of relationship observed between the ocean climate drivers and the fish and crustacean populations. Specifically, we defined a driver-response relationship as 'non-stationary' if it was better fitted and more consistent with the observed data by two functions during different time periods and consequently, an abrupt change in the response was exhibited over time, even in the face of similar driver magnitudes. By contrast a 'stationary' relationship is described by a single function throughout the entire period of observation (Ciannelli et al., 2004). First, the stationary hypothesis was formulated as follows using a GAM:

$$TS_t = \alpha + s_1(D_t) + s_2(SSB_t) + \varepsilon_t \tag{1}$$

where the biological time series (TS) during each year (t) is estimated with an intercept (α), a smooth function (s) of the climate-ocean driver (D; i.e. PDO or GoA SST) and a normally distributed error term (ε). In the case of the recruitment time series (Table 1), a second smooth function of spawning stock biomass (SSB, data available from AFSC stock assessment reports; www.afsc.noaa.gov/refm/stocks/assessments.htm) was included in the model to account for possible density-dependent effects. Second, an extension of GAM known as Threshold Generalized Additive Models (TGAM), was fitted allowing the smooth function to change before or after a threshold value:

$$TS_t = \begin{cases} \alpha_1 + s_1(D_t) + s_2(SSB_t) + \varepsilon_t, & \text{if } t < y \\ \alpha_2 + s_3(D_t) + s_2(SSB_t) + \varepsilon_t, & \text{if } t \geq y \end{cases} \tag{2}$$

The threshold year (y) that separates different periods with different responses to the driver was sought by running TGAM for all possible threshold values (years in the time series) between the 0.2 lower and the 0.8 upper quantiles (number of threshold years tested depended on the length of the time series) and selected by minimizing the Akaike Information Criterion (AIC) of the model. A second smooth function of SSB was also included in this model only for the recruitment time series (Table 1).

Since the AIC does not properly account for the additional parameter used in the threshold formulation (i.e. time), comparisons and model selection between GAM and TGAM were performed by computing the genuine Cross Validation (gCV) score (Ciannelli et al., 2004). The gCV is the average of squared predicted errors, calculated by removing one data point at a time from the original time series and predicting the response of the deleted case from the model fitted to the remaining data. The AIC was only considered as a measure of goodness of fit when gCV values between competing models were very similar. To avoid model overfitting, the number of knots used in each of the GAM and TGAM splines were kept to a maximum of four. Residuals were checked for potential deviation from the normality assumption, homogeneity of variance and other anomalies, including temporal autocorrelation.

2.4. Assessing synchronous changes as a community response

We investigated whether the changes in the response to ocean climate drivers occurred synchronously across all the populations as a community response. We searched for the threshold year that represented a change in relationship between both SST and PDO and biological productivity, across all the population time series. Therefore, we created an indicator variable (PT) that splits the time in two periods for each population: one before and one after a selected threshold year. There are as many terms in the model as possible combinations of populations and time periods (i.e. population 1-period 1, population 1-period 2, population 2-period 1, population 2-period 2, etc.), and for each PT term, a different smooth is fitted to estimate the response of each population and time period to a given driver (D; i.e. GoA SST or PDO). Therefore, to reflect a synchronous response, all populations included the same threshold year. While a population-specific threshold year was allowed in the asynchronous mode and thus, different time periods among populations. Accordingly, the synchronous community model was formulated as follows:

$$TS_{i,t} = PT_t * \alpha_i + s_{1,i,t}(D_t * PT_t) + \varepsilon_{i,t} \tag{3}$$

where i represent each biological population and t indicates the year. In the synchronous non-stationary community model, the term PT does not depend on the population (i), but only on year (t). To avoid model overfitting, the number of knots were kept to a maximum of four. Since the community model presented positive autocorrelated residuals, we allowed for first-order autocorrelation in the error term by estimating population-specific first-order autoregressive coefficients φ_i, i.e. $\varepsilon_{i,t} = \varphi_i \varepsilon_{i,t-1} + \delta_{i,t}$ where $\delta_{i,t} \ N(0, \sigma_i^2)$. To search for the synchronous threshold year in a similar way as in the TGAM approach (2), we fitted the community model for every possible year between 0.2 lower and 0.8 upper quantiles as the threshold year that defines the time periods in the indicator variable PT. The model that minimized the AIC was selected as the one statistically supporting the common threshold year for a non-stationary, synchronous community response.

To address whether the non-stationary and synchronous (GAM as in Eq. (3)) community response to SST (PDO) was more consistent with the community data than other formulations, we compared model (3) with its corresponding stationary model formulation:

$$TS_{i,t} = \alpha_i + s_{1,i}(D_t) + \varepsilon_{i,t} \tag{4}$$

and with the non-stationary and non-synchronous community model:

$$TS_{i,t} = PT_{t,i} * \alpha_i + s_{1,i,t}(D_t * PT_{i,t}) + \varepsilon_{i,t} \tag{5}$$

The non-synchronous model (5) is no longer forced to have a similar threshold year across all populations. Instead the years are assumed to be the same as those found in the single population models (2). To compare the different community models (3–5), we used the gCV values calculated on 500 iterations by removing 10% of the data each time. In every iteration, data from the same years were removed in all populations. Because the model included a lag-1 autocorrelated error structure, the data from years that were removed were still kept in the calibrating data but were assigned a weight of zero, so they did not contribute to the parameter estimates. The community response approach was performed using only the period with complete observation in all populations (1975–2010) to avoid any possible uncertainty and bias introduced by the estimation of missing values, and to make data comparable with those used for the PCA. SSB was not included in the community responses because it was not available for all population time series.

2.5. Community response with PCA analyses

We contrasted the result of the prior analyses with those obtained using PC scores as response variables. PCA summarized most of the
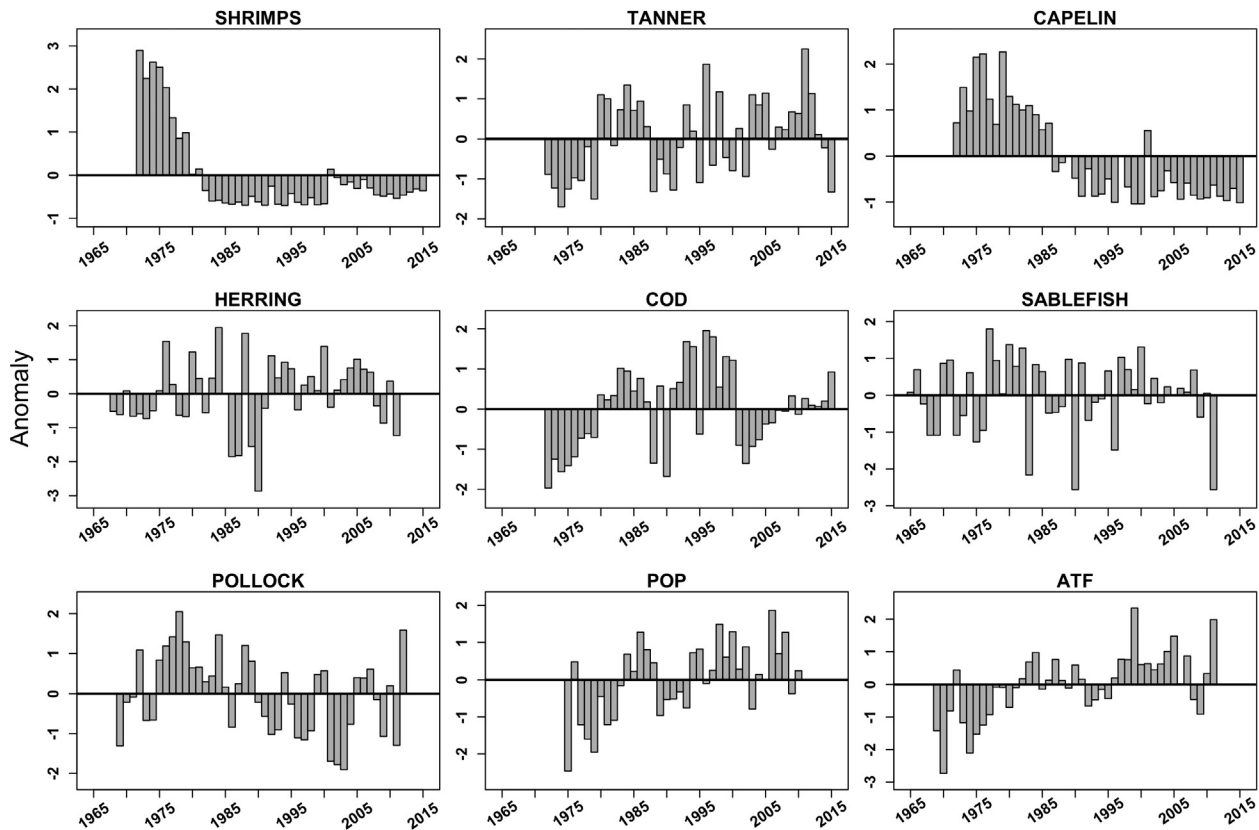
Fig. 1. Normalized time series of biomass (shrimp, Tanner crab, capelin, herring and Pacific cod) and recruitment (sablefish, pollock, Pacific ocean perch, and arrowtooth flounder) of the Gulf of Alaska populations. Abbreviations: COD, Pacific cod; POP, Pacific ocean perch; ATF, arrowtooth flounder.

variance from all populations into several new time series that represents the shared community variability. PCA produced three outcomes: (a) loadings, which describe the influence of each time series on the resulting community response; (b) PC scores, which define the temporal pattern of the community response that describes the largest portion of shared variability; and (c) eigenvalues showing the percent of variance explained by each PCA axis. PCA was conducted only for the period with complete data for all populations (1975–2010). Then, the TGAM formulation (2) was fitted on the PC data to identify the threshold year in the community, as described above, in which the response to GoA SST (PDO) changed.

All analyses were performed using R Statistical Computing Software (v.3.11; http://www.R-project.org/) and the *mgcv* (Wood, 2006) library.

3. Results

Time series of fish and crustacean populations in the Gulf of Alaska were highly variable in terms of duration and the presence or absence of mid- to long-term trends (Fig. 1). While abrupt changes in some population abundance, such as shrimp, capelin or arrowtooth flounder, were observed in the late 70s and early 80s, most of the populations exhibited high inter-annual variability with no apparent clear change of mean values.

For the period 1950–1988, monthly values of North Pacific SST EOF1 were correlated with the PDO index (r = 0.91, P < 0.0001), but not correlated with the NPGO (r = 0.09, P = 0.40), as expected under the separation of axes in the EOF analyses used to define the PDO and NPGO. During 1989–2012, however, while the PDO remained highly correlated with SST EOF1 (r = 0.89, P < 0.0001), the NPGO was also significantly correlated with this first axis of SST variability (r = 0.57, P < 0.001; Fig. 2).
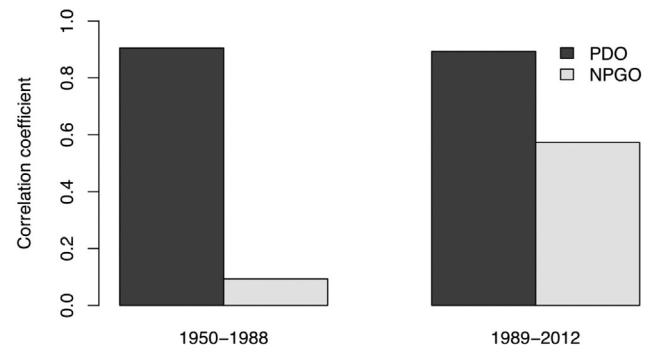

Fig. 2. Changing prominence of the NPGO pattern in North Pacific climate: correlations with EOF1 of North Pacific SST before and after 1988/1989. Only the PDO was significantly correlated with EOF1 prior 1988/89 (*p* < 0.0001); both the PDO and NPGO are correlated with EOF1 after 1988/89 (*p* < 0.001).

3.1. Detecting non-stationary relationships

Model comparisons among stationary (GAM) and non-stationary (TGAM) formulations clearly supported the non-stationary relationship between GoA SST (PDO) and the fish and crustacean populations of the GoA (Table 2). When a threshold non-stationary model better fit a population time series, there were several threshold years that resulted in lower gCV than the stationary model (Supp. 2). The one reported in Table 2 corresponds to the lowest gCV. TGAM presented lower prediction error (gCV) in all cases and better goodness of fit (AIC, except in one case; see Table 2). The strongest non-stationary relationships were observed in shrimp and capelin, where the TGAM formulation drastically dropped AIC and gCV values in comparison to the stationary formulation. However, differences between the two model forms were almost negligible in terms of AIC for herring, sablefish and arrowtooth

Table 2

Summary of full and threshold Generalized Additive Models selection. Abbreviations: SST, Sea Surface Temperature; PDO, Pacific Decadal Oscillation; % var, percentage of the variance explained; AIC, Akaike Information Criterion; gCV, genuine Cross Validation. (*) Models that include stock spawner biomass as an additional term.

Population	GAM			TGAM			
	% var	AIC	gCV	Threshold	% var	AIC	gCV
SST							
Shrimp	46.32	104.7	0.73	1981	95.00	7.34	0.22
Tanner crab	8.87	122.81	0.93	1995	43.29	108.94	0.74
Capelin	3.73	126.39	0.97	1986	83.37	57.89	0.40
Herring	8.41	126.59	0.95	1987	17.7	127.81	0.90
Pacific cod	23.56	119.00	0.86	1990	43.16	111.22	0.75
Sablefish*	12.33	109.32	0.96	1983	55.07	101.09	0.69
Walleye pollock*	14.91	110.27	0.94	1989	41.19	98.98	0.78
Pacific ocean perch*	35.71	85.80	0.73	1993	64.68	73.57	0.55
Arrowtooth flounder*	50.01	101.41	0.70	1996	64.61	98.26	0.59
PDO							
Shrimp	31.17	118.26	0.82	1988	94.65	12.01	0.23
Tanner crab	5.35	128.03	0.96	2006	39.27	113.48	0.77
Capelin	0.62	130.48	0.99	1986	83.62	57.97	0.4
Herring	19.39	123.70	0.89	1984	33.94	120.41	0.80
Pacific cod	22.70	122.81	0.87	1990	38.77	113.04	0.77
Sablefish*	17.49	106.15	0.93	1974	1.73	103.47	1.03
Walleye pollock*	10.7	110.57	0.96	1989	43.41	97.59	0.76
Pacific ocean perch*	47.50	81.68	0.66	1989	62.72	74.94	0.56
Arrowtooth flounder*	48.11	104.19	0.71	1995	62.49	99.64	0.60

flounder, suggesting that these populations are as likely to present a stationary response to GoA SST (PDO) forcing as they are to exhibit non-stationary dynamics. The relationship of GoA SST-Pacific cod and that of PDO-Pacific Ocean perch also displayed small differences between the two model formulations. After the inspection of the model trends (e.g. presence of parallel trends), confidence intervals and residual patterns, we concluded that the relationships of herring, sablefish and arrowtooth flounder with both GoA SST and PDO were better fitted with the stationary models despite the fact that these models showed slightly higher values for AIC, gCV and lower explained variance (Table 2, Supp. 3). The additional inspection of threshold year selection (Supp. 2) supported the conclusion that stationary behavior is a more likely response in these three species since most of the TGAM models tested presented higher AIC values than the equivalent GAM. In order to avoid model overfitting and mistaken inference, we used the most parsimonious models, i.e. stationary GAM, for these three species. Most of the populations displayed a threshold year (i.e. year in which relationship with climate-ocean driver changed) centered in the late 80s or early 90s for both drivers, GoA SST and PDO. However, thresholds differed for each population, but also changed in some populations based on the covariate included in the model formulation (PDO vs GoA SST). In addition, intercept-only changes in the models were also checked, but the results did not improve over those presented for TGAM.

For each population, the best model describing productivity in relation to GoA SST, whether stationary or non-stationary, was plotted in Fig. 3. Very similar results were observed for the relationship between biological productivity and the PDO (Supp. 4). Three different behaviors were observed among the populations: (1) Populations showing stationary relationships with GoA SST, such as herring, sablefish and arrowtooth flounder. A positive linear relationship with GoA SST is evident in these three particular cases, although it was not statistically significant in any case (p-values = 0.056, 0.408 and 0.066, respectively). (2) Non-stationary relationships with opposite trends between periods, as observed in Tanner crabs and walleye pollock. These populations changed from a first period with a positive relationship with

GoA SST (Fig. 3, gray lines) to a second period with a negative relationship (Fig. 3, blue lines). (3) A different pattern of non-stationary relationships was detected for shrimp, capelin, Pacific cod and Pacific ocean perch. While a positive or negative relationship with GoA SST was displayed in the first period, the influence of SST on the productivity of these populations was nearly zero in the second period of time.

### 3.2. Assessing synchronous changes as a community response

Results from the synchronous community model indicated similar changes in the response to GoA SST (PDO) as the population-level approach. The synchronous community model comparison for threshold year selection (i.e. year at which community response to GoA SST (PDO) change based on AIC) defined 1987 as the time separating the before and after regimes for both drivers, GoA SST and PDO (Fig. 4). Thus, 1987 was used to define periods 1 and 2 in the population-period term for the synchronous community model. Significant effects of GoA SST (PDO) on the productivity were detected in six (five) of the nine populations, mainly in the first period (1975–1987). In the second period (1988–2010), the p-values increased remarkably, indicating the GoA SST (PDO) effect disappeared (Fig. 5). However, significant non-stationary dynamics were observed for arrowtooth flounder and herring but not for capelin, a result that is in partial disagreement with the individual population models. The models that fitted the synchronous community response to GoA SST (PDO) presented very low 0.11 (0.08) R^2 values. Thus, when comparing this model with the stationary and the non-stationary and non-synchronous community models (Table 3), we found that for GoA SST the latter (i.e. the one with a population-specific threshold) had the lowest gCV and the highest selection probability in 500 iterations. In the PDO models, the stationary formulations presented the lowest gCV values, however the non-stationary and non-synchronous model formulation was selected in most of the 500 iterations (Table 3).

3.3. Community response with PCA analyses

The variability of the nine populations was summarized in a reduced number of time series using principal component analysis (PCA), which describes the community trends over time (scores, Supp. 5). PC1 represented 32.5% of total variability across populations, while PC2 only accounted for 16.7%. In PC1, the strong loadings for shrimp and capelin (negative sign), indicated a strong association of these populations with the total community variability (Supp. 5). Variability in herring and sablefish were not well represented by PC1 or PC2 (Supp. 5), while the rest of populations showed similar loading values (positive sign). PC2 also loaded strongly on shrimp (Supp.5) and arrowtooth flounder, which did not show any particular trend over time (Fig. 1). The non-stationary models (TGAM) applied on the community trends (PC1 and PC2) showed the exactly same response to GoA SST and PDO in the community (Fig. 6). PC1 displayed two clearly different and robust trends before and after 1988, describing a strong positive relationship between the covariate and the community variability in the first period, which diminished to a near zero slope in the second period (Fig. 6). However, the trends observed in PC2 were less robust (based in confidence intervals, Fig. 6.), showing a positive relationship that changed around the mid-80s to a different shape (Fig. 6). Additionally, PCA based community models explained a higher portion of the variance and exhibited much lower predicted errors in TGAMs compared with those using GAMs (Supp. 6).

4. Discussion

The influence of North Pacific climate shifts on the production and composition of marine communities has been frequently explored (Hare and Mantua, 2000; Litzow, 2006; Litzow et al., 2014; McFarlane et al.,
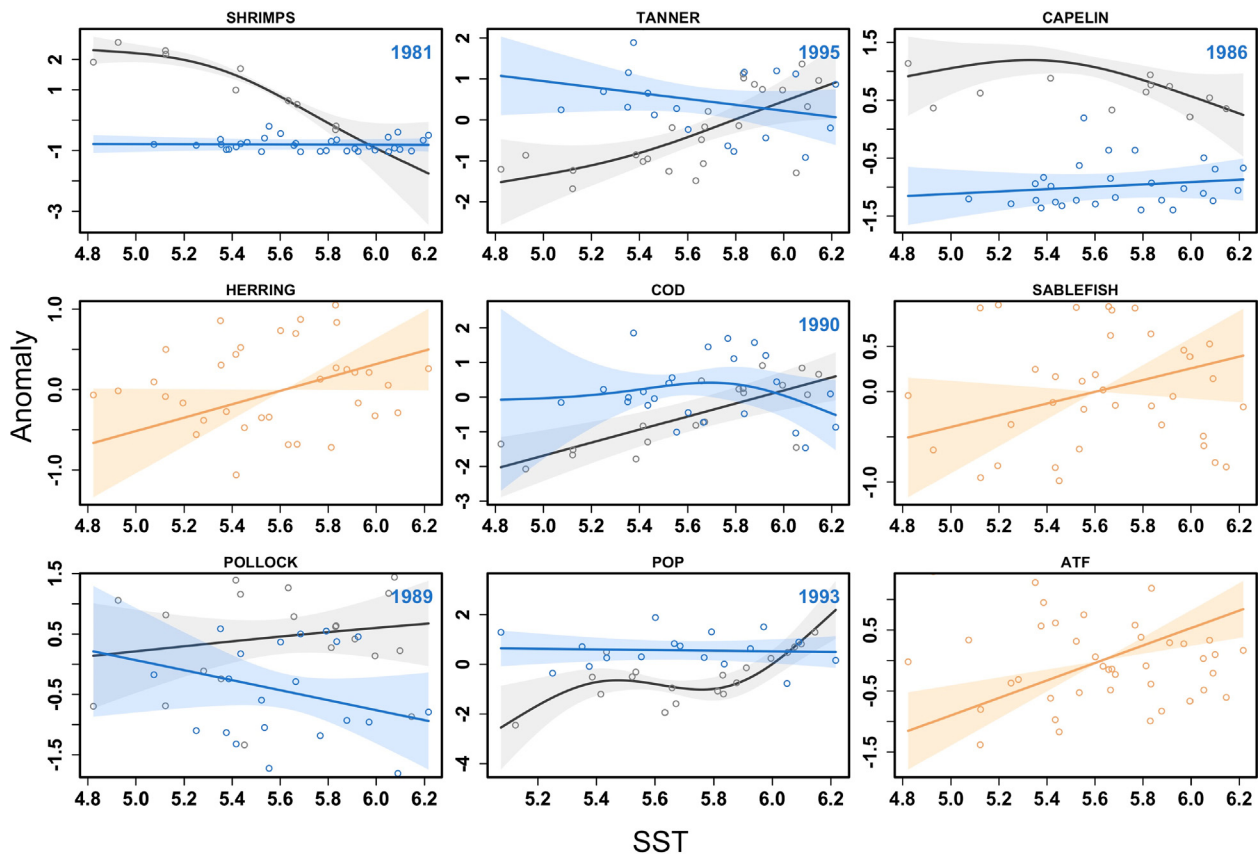
Fig. 3. Best model for each population productivity or abundance index, showing the relationship with Gulf of Alaska sea surface temperature (SST). Stationary models (Generalized Additive Models) are shown in orange, while the non-stationary models (Threshold Generalized Additive Models) present two colors: first time period in gray and second period in blue. The threshold year dividing these two periods is in the upper-right corner of the plot. In all plots, shaded areas denoted 95% confidence intervals, x axes display SST values in degrees Celsius and y axes display temperature effects on the anomalies of fish and crustacean standardized indices of productivity or abundance. Circles represent model partial residuals. Abbreviations: COD, Pacific cod; POP, Pacific ocean perch; ATF, arrowtooth flounder. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
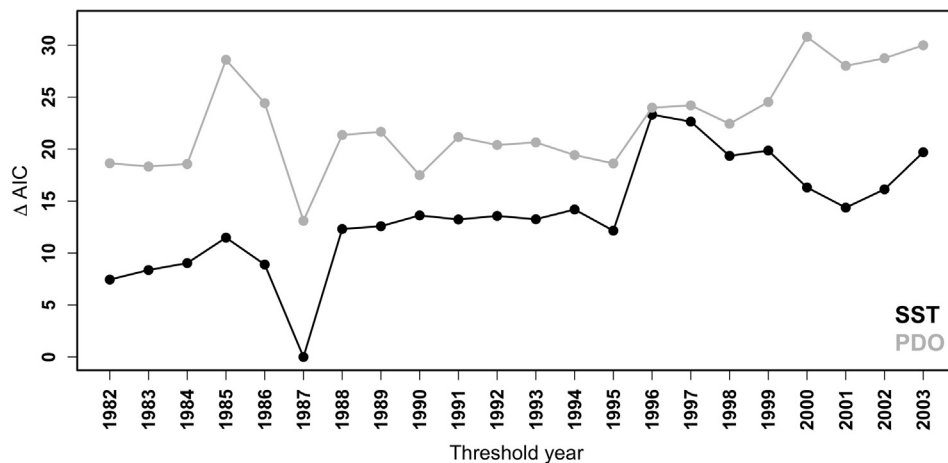
Fig. 4. Threshold year selection for the synchronous community Threshold Generalized Additive Model including either Gulf of Alaska sea surface temperature (SST) or Pacific Decadal Oscillation index (PDO) as the explanatory variable. Y-axis presents the increment in Akaike Information Criterion.

2000; Overland et al., 2008). However, biological responses to such shifts may also include characteristics other than changes in productivity or composition. For example, biological responses might also fall into other categories, such as spatial displacement in the population distribution or changes in the "governing rules" or system functioning (Conversi et al., 2014; Overland et al., 2008). We demonstrated that most of the nine studied fish and crustacean populations in the Gulf of Alaska (GoA) responded to variability in local temperature and basin-

scale climate (i.e., the PDO) differently in periods before and after an objectively identified 'threshold year' that ranged from early 80s to early 90s. Six of the nine GoA fish and crustacean populations investigated here mainly exhibited a non-stationary behavior or an abrupt change in the relationship with temperature and climate over time, and three of them showed a stationary response to climate forcing. These contrasting behaviors were also observed in other studies (Beaugrand, 2015; Hsieh et al., 2005). Typically, the PDO pattern loads more
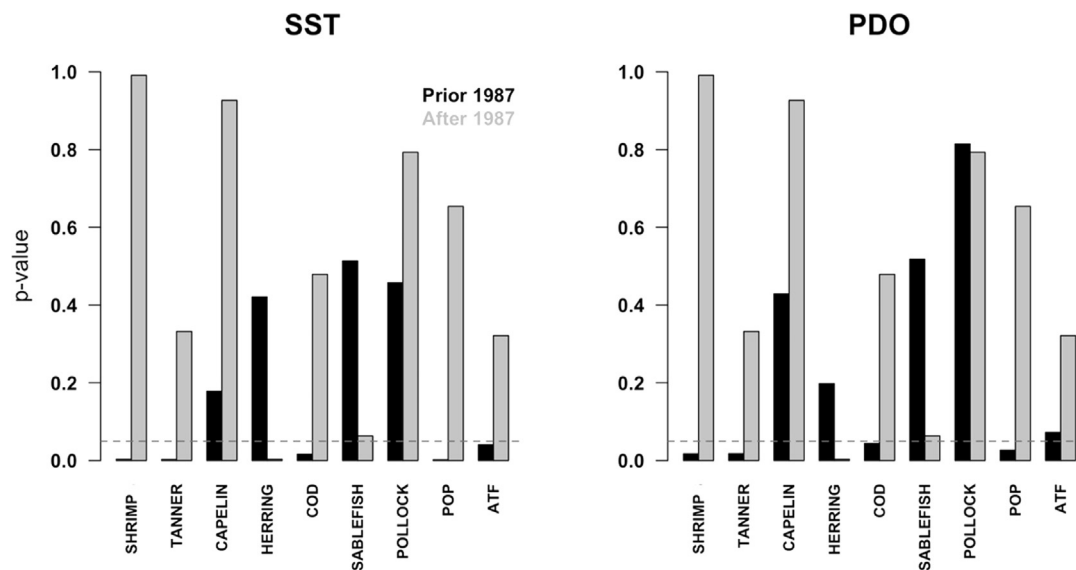
Fig. 5. Summary of the Generalized Additive Models for the synchronous community response including either Gulf of Alaska sea surface temperature (SST) or Pacific Decadal Oscillation index (PDO) as the explanatory variable. Effects of SST (PDO) on each population is defined by the p-values, with time periods of the non-stationary response defined by data prior 1987 (black bars) and after 1987 (gray bars).

Table 3

Comparison of stationary and non-stationary, synchronous and asynchronous formulations for the community model based on the mean squared error (gCV) at 500 iterations and, including either Gulf of Alaska sea surface temperature (SST) or the Pacific Decadal Oscillation index (PDO) as the explanatory variable. The selection column indicates how many times each model was selected as the best fit in the 500 iterations; 14 iterations did not converge for the PDO models. Synchronous threshold refers to 1987 and asynchronous to the different threshold obtained for each population using Threshold Generalized Additive Models (see Fig. 3 and Supp. 2).

Model	Threshold	Driver	gCV	Selection
Stationary	–	SST	0.87	138
Non-stationary	synchronous	SST	0.88	165
Non-stationary	asynchronous	SST	0.83	197
Stationary	–	PDO	0.88	150
Non-stationary	synchronous	PDO	1.07	134
Non-stationary	asynchronous	PDO	1.51	202

strongly on the GoA region than does the NPGO pattern (Di Lorenzo et al. 2008). However, the non-stationary responses of GoA taxa to SST and PDO that we found suggest a reduced importance of the PDO shaping the variability of GoA biological communities from the late 1980s to 2012. The proposed increase in North Pacific climate variance explained by the NPGO since the late 1980s (Di Lorenzo et al., 2010; Kilduff et al., 2015; Sydeman et al., 2014; Yeh et al., 2011) is clearly reflected in the increased correlation between the NPGO and EOF1 of North Pacific SST (Fig. 2). Evaluation of the timing of the increasing correlation between the NPGO and SST EOF1 suggests that this change was consistent with the 1988/89 North Pacific climate shift (Litzow et al. 2018). Our methodological approach supports an objective, data-driven detection of non-stationary relationships and timing associated with climate variability in the North Pacific. However, this non-stationary dynamic did not arise synchronously as a community response across the different populations.

In general, the different model results support a widespread non-stationary response of GoA taxa, considering that not all the populations are expected to exhibit similar sensitivities to shifts in physical climate. But when present, these responses might vary among populations, as also observed in previous studies (Beaugrand, 2015; McFarlane et al., 2000). The magnitude and timing of the community response depends not only on the sign and magnitude in the climate shift

(Boulton and Lenton, 2015; Mueter et al., 2007), but also on the species composition (Beaugrand, 2015). Thus, community responses might be also conditional on the changes in the complex dynamics that arise when responses at population levels are compiled. For example, food web interactions may mediate variability in the abundance and recruitment of species considered here. Most of the taxa included in the GoA community analysis are trophically linked. For instance, Pacific cod, walleye pollock and arrowtooth flounder all prey on shrimp, crabs and forage fish (Anderson and Piatt, 1999; Zheng and Kruse, 2000 and references therein). Species interactions might be also sensitive to changing climate and thus, changes in water temperature might limit encounters between prey and predator species due to different thermal tolerances, changing the top-down dynamic (Conversi et al., 2014; Litzow and Ciannelli, 2007). Additionally, temperature is only one of many environmental properties that influence fisheries productivity; but it also indexes on several other variables that also affect productivity, such as mixed layer depth, wind stress or stratification (Litzow et al., 2018; see also more details below).

Recognition of non-stationary climate-biology relationships can sometimes be hampered by the use of PCA for identifying common trends in communities. This method is very useful to reduce dimensionality when analyzing multiple time series and can represent substantial variability in the full data matrix under consideration. However, it also presents potential downsides due to the underlying assumptions that usually receive little consideration (Planque & Arneberg, 2017). Namely, aggregated response analyses require time series equal in length for each component species, which is uncommon in biological data; analytical approaches to deal with missing values might misrepresent the actual response of the biological community. Additionally, when only few species covary in time and exhibit long-term trends, the PC scores will reflect the dynamics of the (few) covarying species, and one must be cautious to extrapolate PCA results at the community level (McFarlane, King & Beamish, 2000; Litzow, Mueter & Hobday, 2014; Planque & Arneberg, 2017). Lastly, PCA assumes stationary characteristics (i.e., constant mean and variance over time) in the composing time series since it is based on the linear correlation among variables and so requires a stable correlation matrix over time. In such instances when assumptions are violated, PCA can provide biased results (Lansangan & Barrios, 2009; Zhao & Shang, 2016). For those reasons, the PCA approach in this study did not provide a satisfying representation of community dynamics and was not useful to
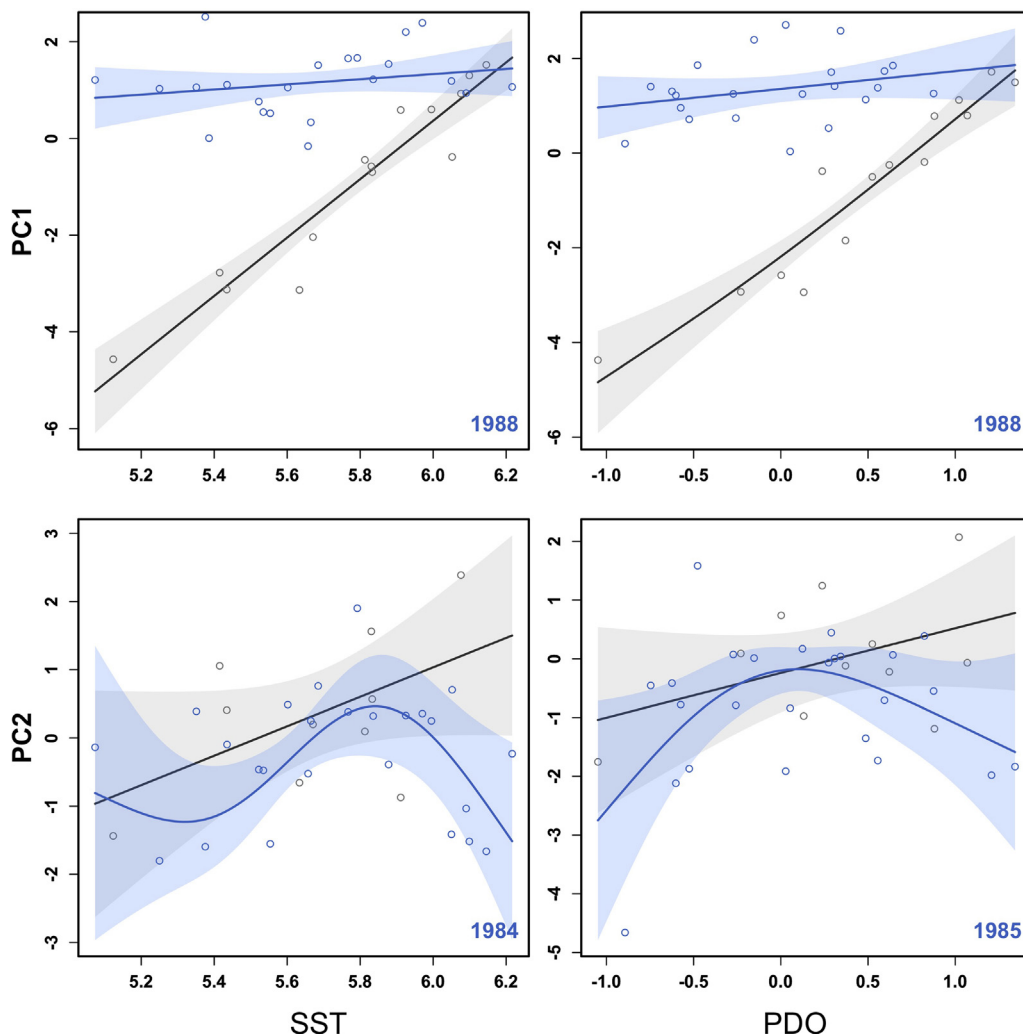
Fig. 6. Threshold Generalized Additive Models (TGAM) fitted on the Gulf of Alaska community aggregated variability obtained by Principal Component Analysis. The first time period is displayed in gray and the second period in blue. The threshold year dividing these two periods is in the lower-right corner of the plot. The shaded areas denoted 95% confidence intervals. Circles represent model residuals, x axes display GoA Sea Surface Temperature (SST) values in degrees celsius and Pacific Decadal Oscillation index (PDO) values: y axes display the effect of these variables on PC1 and PC2, which are unitless. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detect synchronous changes among biological time series as a community response. These results highlight the importance of carefully consider assumptions before applying any statistical technique for inference and validate and confirm the obtained results with different approaches.

While we rejected the hypothesis of a synchronous change in the community response to GoA SST (PDO), we did observe shifts in the response to GoA SST (PDO) in many taxa in the late 80s or early 90s. It has long been recognized that the 1988/89 shift in North Pacific climate was not a simple reversal of the PDO phase to the conditions previous to the 1976/77 shift, and differences in both the physical characteristics and the ecological responses associated with these shifts have been highlighted (Di Lorenzo et al., 2008; Hare and Mantua, 2000; Yeh et al., 2011). The 1988/89 climate shift coincided with a greater portion of SST variance becoming associated with the NPGO (Fig. 2) and, may coincide with a shift in the relative importance of leading axes of natural climate variability (Di Lorenzo et al., 2008; Johnstone and Mantua, 2014; Litzow et al., 2014; Yeh et al., 2011). An important consequence of this large-scale change for the GoA ecosystem was the decline in Aleutian Low variance and decline in the strength of covariance among individual climate variables. Prior to the late 1980s, both SST anomalies and the PDO were strongly correlated with the leading axis of PC1 for six climate variables thought to play a central role in regulating GoA ecological variability; after the late 1980s these correlations between the SST or PDO and GoA climate variability weakened and became non-significant (Litzow et al. 2018). It has long been proposed that correlations between SST and fish population dynamics in

the northeast Pacific do not simply result from direct temperature effects on fish physiology, but also arise from the propensity of SST to be correlated with a range of ecologically important climate variables (Mueter et al., 2002). Under this view, when correlations between SST (PDO) and other climate variables acting on a population change, relationships between SST (PDO) and the population are also expected to change. Our results support this hypothesis for the GoA populations we examine, and demonstrate that SST-biology and PDO-biology relationships are non-stationary in this system and cannot be modeled as fixed properties over multidecadal time scales. These findings highlight an important consideration for the use of the PDO and NPGO indices over multidecadal time scales. The PDO and NPGO patterns are statistical summaries of climate that arise from multiple independent physical processes. Because these generating processes operate on independent time scales, the sets of physical conditions mapping onto the PDO and NPGO are expected to change over time (Newman et al., 2016). Several other studies have noted apparent examples of non-stationary climate-biology relationships in the northeast Pacific around the late 1980s, characterized by changes in the sign or magnitude of ecological responses to either local environmental variables or the PDO/NPGO indices (Kilduff et al., 2015; King et al., 2011; Miller and Sydeman, 2004; Schmidt et al., 2014). In paleoecology, changing relationships among physical variables are recognized as producing surprising population and community responses that are poorly constrained by models based on contemporary ecosystems (Williams and Jackson, 2007). The increasing association between the NPGO and EOF1 of North Pacific SST after 1988/89 is believed to correspond with

a change in the nature of atmospheric teleconnections between the tropics and extra-tropics that are important drivers of decadal ocean climate variability in the North Pacific (Yeh et al., 2009, Di Lorenzo et al., 2010). As noted earlier, this change was also associated with decreasing variance in Aleutian Low SLPa values, and changing relationships between SST and other environmental variables in the GoA (Litzow et al., 2018). Given these changing relationships among important physical drivers, and coincident changes in biological responses to SST and PDO variability, we propose that the post-1988/89 era might usefully be viewed as a novel climate when compared with earlier decades.

The approach we propose to address non-stationary responses in biological communities is based on robust statistical techniques that have been developed and implemented several times already (Ciannelli et al., 2004; Liu et al., 2011). However, the application to community-wide data is novel, and will contribute to improving inferential analysis and the comprehension of climatic-ecological shifts and thresholds in a research field particularly relevant for near-future climate change conditions. As is always the case with observational studies, we cannot rule out alternate causality driven by factors that are not considered in our analysis, such as changes in trophic structure, fisheries exploitation effect or changes in the demographics of a population (Rouyer et al., 2012). Our analyses cannot resolve the mechanisms influencing climate-productivity relationships, but have demonstrated that such relationships may change over time in ways that are species-specific and not easily predicted. Understanding how populations and communities respond to climatic variability is critical for predicting the ecological consequences of climate change and for anticipating efficient management approaches for commercially exploited species and marine ecosystems.

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2019.04.002.

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